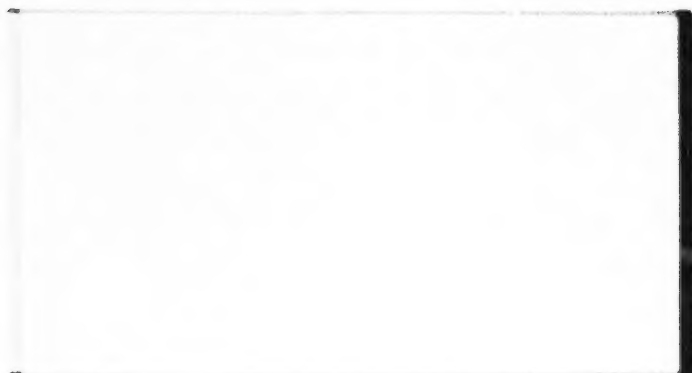




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**FACTORS AFFECTING STUMP
SPROUTING AND ROOT SUCKERING
IN WOODY SPECIES**

Report No 83-234-K

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Chemical Research Department

ABSTRACT

Many species of woody plant produce sprouts on the lower stem and root collar and/or suckers on the roots after death of the parent top as a result of cutting, fire or disease. Several factors influence the number and rate of growth of such sprouts after decapitation of many tree species including tree age, diameter and height of the cut stump, the time interval between successive cuttings and the time of year of cutting. Root suckering is influenced by soil temperature and the season of cutting. Following decapitation, the plant growth regulators cytokinin, gibberellin and auxin influence sprout and sucker development.

job	file	date	report no.
740634-621-031	834.1	July 29, 1983	83-234-K



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EXECUTIVE SUMMARY

FACTORS AFFECTING STUMP SPROUTING AND
ROOT SUCKERING IN WOODY SPECIES

G.P. Arron
Biologist
Chemical Research Department

Stump sprouting and root suckering of woody plant species are a major problem to Ontario Hydro on rights-of-way where line clearance work must be carried out periodically. At present, various methods, both mechanical and chemical, are used in an attempt to reduce the growth of stump sprouts and root suckers. If it were possible to reduce the development of sprouts and suckers after clearcutting and routine clearing operations, in terms of the numbers of sprouts and suckers produced and their rate of growth, then routine line clearance work could be conducted less frequently.

Many factors influence the number and rate of growth of stump sprouts and root suckers that develop on woody species after removal of the parent top. In some tree species, stump sprouting is affected by tree age, diameter and height of the cut stump, the time interval between successive cuttings and the time of year of cutting. Root suckering is influenced by soil temperature and the time of year when the stem is cut.

In many tree species decapitation in the winter leads to vigorous sprout and sucker development. If at all feasible, it would be better to cut such species in the summer during routine line clearance operations since the number of sprouts and suckers that develop and their rate of growth will be lower.

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research division**

To Mr. F.J. Kee
Director of Research

**FACTORS AFFECTING STUMP SPROUTING AND
ROOT SUCKERING IN WOODY SPECIES**

1.0 INTRODUCTION

Stump sprouting and root suckering of woody plant species are a major problem to Ontario Hydro on rights-of-way where line clearance work must be carried out periodically. Any rights-of-way management program which successfully reduces the growth (in terms of height as well as number and volume) of sprouts and suckers would be advantageous.

Much of the information discussed in this review has been gleaned from the excellent reports of Blake (1981b) and Blake and Raitanen (1981) which were produced as a result of the recent interest in forest products as a source of biomass for alternative sources of energy. These reports describe the coppice method of regeneration, where trees are cut to stump height, and the sprouting of buds on stump and roots results in fast rates of growth (ie, high biomass production).

In any discussion of stem and stump sprouts and root suckers, the terms sprout and sucker should be carefully defined. In the past there has been some confusion as to the correct term to use to describe a shoot which forms on the root of woody plants, and both root sprout and root sucker have been used. In this review the latter term will be used (Kozlowski, 1971; Kramer and Kozlowski, 1979) since it cannot be confused with sprouts that develop on the stem and cut stump.

**2.0 ASEXUAL REPRODUCTION OF WOODY PLANTS
BY SPROUTING AND SUCKERING**

Sprouting is a typical response to sudden death of parent tree tops as a result of fire or cutting or to disease and physiological disorders (Kramer and Kozlowski, 1979). The capacity of woody plants to produce sprouts is of tremendous importance to their survival. Sprouts which originate from root collars and the lower part of the stem usually arise from previously existing dormant buds (Kramer and Kozlowski, 1979). The differences

between dormant buds and adventitious buds (mentioned below) are outlined in Appendix A. The stump sprouts which arise on the root collar or lower stem constitute the most important type of vegetative reproduction of hardwood forest stands. For example, many of the New England hardwood forests and most of the oak forests of Pennsylvania originate from stump sprouts (Kramer and Kozlowski, 1979). Stool sprouts develop from adventitious buds which arise from between the bark and wood of stumps. Ordinarily, stool sprouts are short-lived and of no real importance in vegetative propagation.

After disturbances of hardwood forest stands by heavy cutting or fire, some species of trees regenerate largely by root suckers which originate from adventitious buds on roots of the residual and cut trees (Kozlowski, 1971; Kramer and Kozlowski, 1979). The importance of opening of aspen (*Populus tremuloides*) stands to productions of root suckers was shown by data of Stoeckeler and Mason (1956). They observed over 2800 aspen sprouts per acre on open sites following heavy cutting and as few as 377 sprouts per acre in undisturbed stands.

3.0 FACTORS AFFECTING STEM AND STUMP SPROUTING

3.1 Sprouting in Angiosperms and Gymnosperms

Capacity for sprouting is common in angiosperms and rare in gymnosperms (Kramer and Kozlowski, 1979). There is also considerable variation among species of angiosperms. A list of wood species (all angiosperms) that sprout and/or sucker is given in Table I. Little (1938) observed that white oaks (*Quercus alba* L.) and post oaks (*Q. stellata* Wang.) produced more but shorter sprouts per stump than did black oaks (*Q. velutina* L.) and scarlet oaks (*Q. coccinea* Muenchh). Chestnut oak stumps (*Q. prinus* L.) gave rise to nearly as many stems as did those of white oak, yet the sprouts were more vigorous at the end of the first season than were those of the black oak group. Before the fourteenth year, vigor, as measured by height, was greatest for scarlet oak followed by black oak. Persistence of sprouts ran in the following order: post oak, white oak, chestnut oak, black oak, scarlet oak. The references by Little (1938) to vigor and height of growth from the stump are pertinent to control of woody growth on rights-of-way by Ontario Hydro in that the factor which determines when trees have to be cut or pruned is the distance from the top of the tree to the line. Thus the number of sprouts that develop on the stump may not be important, but the height of the sprout(s) is.

TABLE I

PARTIAL LIST OF WOODY SPECIES THAT FORM
STUMP SPROUTS AND ROOT SUCKERS

Species	Root Sucker Formation	Stump Sprout Formation
Trembling aspen (<i>Populus tremuloides</i> Michx.)*	X	X
Balsam poplar (<i>P. balsamifera</i> L.)*	X	X
Large-tooth aspen (<i>P. grandidentata</i> Michx.)	X	-
Eastern cottonwood (<i>P. deltoides</i> Bartr.)	X	X
Sugar Maple (<i>Acer saccharum</i> Marsh.)*	-	X
Silver maple (<i>A. saccharinum</i> L.)*	-	X
Red maple (<i>A. rubrum</i> L.)*	-	X
Manitoba maple (<i>A. negundo</i> L.)	-	X
White ash (<i>Fraxinus americana</i> L.)*	-	X
Black ash (<i>F. nigra</i> Marsh.)	-	X
Basswood (<i>Tilia americana</i> L.)	-	X
Willows (<i>Salix</i> spp)*	X	X
White birch (<i>Betula papyrifera</i> Marsh.)*	-	X
Yellow birch (<i>B. alleghaniensis</i> Britt.)	-	X
Black cherry (<i>Prunus serotina</i> Ehrh.)	-	X
Pin cherry (<i>P. pensylvanica</i> L.f.)*	-	X
White oak (<i>Quercus alba</i> L.)	-	X
Red oak (<i>Q. rubra</i> L.)*	-	X
White elm (<i>Ulmus americana</i> L.)*	-	X
Black locust (<i>Robinia pseudoacacia</i> L.)	X	X

* Species which are a problem for Ontario Hydro on rights-of-way.

Above list compiled with the assistance of B. Allen and E.J. Medicky.

All angiosperms do not sprout equally throughout their ranges. For example sugar maple (*Acer saccharum* Marsh.) beech (*Fagus* spp) and hophornbeam (*Ostrya virginiana* (Mill.) K. Koch) sprout vigorously in the northern but not in the southern part of their ranges. Many oaks, however, sprout vigorously through a greater part of their range (Braun, 1950).

Regeneration by sprouts is relatively unimportant in gymnosperms, although a few species sprout prolifically, especially after fire. Gymnosperms with good sprouting ability include redwood (*Sequoia sempervirens* (D. Don) Endl.) pitch pine (*Pinus rigida* Mill.) shortleaf pine (*P. echinata* Mill.) and pond pine (*P. serotina* Michx.) (Kramer and Kozlowski, 1979).

3.2 Effect of Nutrient Status on Sprouting

Nitrogen, mineral nutrients and moisture supply are all, at times, critical in the growth of a plant. Although early studies (eg, Zon, 1907) suggested that they were crucial in influencing the growth of sprouts in a particular species, more recent studies have shown them to be of rather less importance (Wenger, 1953; Blake and Raitanen, 1981). Much of the recent work has concentrated on application of fertilizers (nitrogen, phosphorus, potassium) in an effort to increase growth and yield of species used in short rotation forestry projects. Although application of fertilizers does prevent the decline in productivity (ie, biomass of sprouts) which may occur in the second and subsequent rotations (cuttings), the yield of sprouts after the initial cutting does not appear to be increased by application of fertilizer (Heilman et al, 1972). In soils deficient in nutrients, application of fertilizers, particularly nitrogen, may improve sprout growth, and this suggests that a shortage of nitrogen may lead to reduced sprout growth (Jones and Curlin, 1968).

3.3 Effect of Age of Tree, Stump Diameter, and Stump Height on Sprouting

The ability of stumps and root callus to sprout following cutting is usually optimal on sapling-size trees, but may decline in older trees (Maini and Cayford, 1968). In some studies efforts have been made to distinguish between the age of a tree and the diameter of the stem or stump. At first hand there would appear to be a direct correlation between the age of a tree and the diameter of its stem. However, in northern red oak (*Quercus rubra* L.), for instance, stumps sprout prolifically even when parent trees are 100 years of age or older, and these stump sprouts usually become a major stand component following clearcutting of mature red oak stands (Johnson, 1975). Low density multiple-stemmed stands of stump sprout origin thus replace nearby pure high density and single-stemmed red oak stands of seedling origin. Multiple stems of northern red oak often persist for 50 years or more, and consequently the predominant cultural unit is a clump of interactive stems. Although these stems will be considerably younger than the parent tree, the root system of the parent tree may still influence sprout development on them. Kharitonovich (1937) found that in English oak (*Quercus robur* L.) coppice the growth of sprouts was influenced by development of the root system of the parent tree.

In some woody species there does appear to be a correlation between the age of the stump and a loss of ability to form sprouts. In many species there appears to be a critical age beyond which sprouting ability is eventually lost, although this

age may vary greatly from one species to another. Several reports on the effect of the age of a tree on subsequent sprouting are outline in Table II. The sprouting ability of some trees, eg, redwood (*Sequoia sempervirens* (D.Don) Endl.), does not seem to be affected by age (Fritz, 1929).

TABLE II
EFFECT OF AGE OF TREE ON SPROUTING

Species	Comment	Reference
Trembling aspen (<i>Populus tremuloides</i> Michx.)	Sprouting was heavy at all ages and stump size in stands from 70 - 110 years of age	Baker 1918
Trembling aspen (<i>Populus tremuloides</i> Michx.)	Stump and root collar sprouting declines after 8 years beyond which root suckers are favoured	Perala 1979
Redwood (<i>Sequoia sempervirens</i> (D.Don) Endl.)	Very old redwood trees sprout as readily as young trees	Fritz 1929
4 species of white oak (<i>Quercus</i> spp)	60% of 30 - 70 year old oak stumps formed sprouts	McQuilkin, 1975
Mixed hardwood	Large trees sprouted infrequently as sprouting ability had been lost with age	Ostrom 1938
Sugar maple (<i>Acer saccharum</i> Marsh.)	Stump size was more important than stump age for sprouting vigor	Solomon and Blum 1967

Above table adapted from Blake and Raitanen, 1981.

Although it does not hold for all woody species, there does appear to be a correlation between the diameter of the stem (usually measured at breast height:dbh) and the ability to form sprouts. As with tree age, there seems to be some critical diameter above which sprouting ability falls off. The results

from several investigations are outlined in Table III. With both sugar maple (*Acer saccharum* Marsh.) and red maple (*A. rubrum* L.) there was a decrease in the number of sprouts formed on stumps greater than 12 cm and 22 cm in diameter respectively (Solomon and Blum, 1967). The same authors found no correlation between the ability of paper birch (*Betula papyrifera* Marsh.) to form sprouts and the diameter of the cut stump.

TABLE III
EFFECT OF STUMP DIAMETER ON SPROUTING

Species	Comment	Reference
Longleaf pine (<i>Pinus palustris</i> Mill.)	Stumps with ground-line diameters of 3 cm or less produced up to 3x more sprouts than stumps with diameters greater than 3 cm	Farrar 1975
Northern red oak (<i>Quercus rubra</i> L.)	67% of 33 cm diameter stumps produced at least one sprout, while none of the 66 cm diameter stumps produced a sprout	Johnson 1975
Red maple (<i>Acer rubrum</i> L.)	Number of sprouts increased with increasing stump diameter to 22 cm, above this the number of sprouts decreased	Solomon and Blum, 1967
Sugar maple (<i>Acer saccharum</i> Marsh.)	Greatest number of sprouts produced by stumps 12 cm in diameter or less, above this the number of sprouts decreased dramatically	Solomon and Blum, 1967
Paper birch (<i>Betula papyrifera</i> Marsh.)	No obvious correlation between stump diameter and sprouting	Solomon and Blum, 1967
White ash (<i>Fraxinus americana</i> L.)	Direct correlation between the number of sprouts produced and the diameter of the cut stem	Goldsmith and Lees 1982

Stump height had a variable effect on sprouting vigor depending on the species (Blake and Raitanen, 1981). The results from several investigations are outlined in Table IV. In some species a high stump allowed for more sprouting, whereas in other species stump height had no effect on sprouting.

TABLE IV
EFFECT OF STUMP HEIGHT ON SPROUTING

Species	Comment	Reference
Wire (gray) birch (<i>Betula populifolia</i> Marsh.)	Stumps cut low to the ground produced a greater number of sprouts than stumps cut higher	Schrierbeck and Clarke 1940
5 oak species (<i>Quercus</i> spp)	Stump height had little effect on sprouting capacity	Roth and Hepting 1943
Eastern cottonwood (<i>Populus deltoides</i> Marsh.), balsam cottonwood (<i>P. trichocarpa</i> T&G)	No real difference in number, diameter or height growth of sprouts due to stump height	DeBell and Alford 1972
American sycamore (<i>Platanus occidentalis</i> L.)	Total number of live sprouts per stump increased as stump height increased	Belanger 1979
Blackgum (<i>Nyssa sylvatica</i> Marsh.)	High stumps had more than 3x as many sprouts as low stumps	Hook and DeBell 1970
<i>Eucalyptus</i> species	Stump height had no real effect on survival or sprouting of stumps	Dyson 1974

Above table adapted from Blake and Raitanen, 1981.

3.4 Effect of Carbohydrate Reserves on Sprouting

Much of the early work on sprouting of trees concentrated on the relationship between the vigor of sprouting, expressed by the size attained by sprouts in one year, and the amount of reserve carbohydrates in the stump (Wenger, 1953). The expectation was that larger stumps would produce larger sprouts because of the greater amount of reserve carbohydrates. In studies with sweetgum (*Liquidambar styraciflua* L.) Wenger (1953) did not find a positive correlation between sprout growth and reserve carbohydrates in the roots, rather the amount of sprout growth determined the amount of carbohydrates used. More recent work by Blake (1973) and Taylor et al (1982) has confirmed this finding, with similar levels of soluble sugars and starch being found in red river gum (*Eucalyptus camaldulensis* Dehn.) and messmate (*E. obliqua* L'Herit) stumps after decapitation. Stumps of the former sprouted vigorously after decapitation, whilst those of the latter produced healthy sprouts but rapidly become senescent and died. These authors suggested that other factors were involved in "seedlings decline" following cutting.

3.5 Length of Time Between Cuttings, and Its Effect on Sprouting

There is a lot of evidence to suggest that if decapitation of a tree is repeated on a yearly basis, then the amount of sprouts produced will decline with each successive cut (Blake and Raitanen, 1981). DeBell and Alford (1972) found that after the second year of cutting black cottonwood (*Populus trichocarpa* T&G) the sprouts produced grew more slowly, were smaller, more susceptible to wind breakage, and more subject to decay than sprouts produced after the first cut. Lees (1981) reported that, although at least three generations of stump sprouts can thrive on the same regenerating root system of red maple (*Acer rubrum* L.), the period between cuttings should be approximately 30 years. In 18th century Europe it was common to cut oak (*Quercus* spp), ash (*Fraxinus* spp), beech (*Fagus* spp) and chestnut (*Castanea* spp) every 12 to 18 years but this led to root degradation and low shoot vigor (Lees, 1981).

If cutting is repeated after a very short interval, then sprout height may be reduced. Vogt and Cox (1970) reported that in pin oak (*Quercus palustris* Meunch.) a double cutting with a 24-hour interval between the first and second cuttings significantly reduced sprout height. Average sprout height of seedlings cut once was almost three times that of sprouts from seedlings cut twice. These authors made these measurements five weeks after cutting, and it would be interesting to know if these rates of growth were continued in the longer term.

3.6 Effect of Time of Year of Cutting on Sprouting

It has long been recognized that season of cutting has a considerable influence on the vigor of subsequent sprouts, and even that cutting at certain seasons would entirely prevent sprouting (Buell, 1940). The early work of Zon (1907) described how two-year-old sprouts from winter cut white oak (*Quercus alba* L.), black oak (*Q. velutina* Lam.), scarlet oak (*Q. coccinea* Meunchn.) and Spanish oak (*Q. palustris* Meunchn.) were taller than those from summer cut trees. Mattoon (1909) found that sprouts from chestnut (*Castanea dentata* (Marsh.) Borkh.) stumps cut in mid-winter were larger and stronger at the end of the first growing season than were those from stumps cut in May. When dogwood (*Cornus florida* L.) was cut in March, three-year-old sprouts were taller than those on trees cut at other times of the year (Buell, 1940). Cuttings made in July or early August produced sprout clumps with the least maximum height, the least average height of dominant sprouts, the least average width of clump, and the least total length of live sprouts. The total number of sprouts in the clumps was not quite at the minimum for the July cutting, but was close to it (Buell, 1940). This author suggests that dogwood should be cut during the later winter when it is to be reproduced by sprouts.

From the observations discussed above, it is apparent that the production of sprouts following cutting may be described in several ways, ie, the number of sprouts, the height of sprout(s) after a given time and the number of sprouts that survive in the longer term. If one were interested in producing the largest amount of biomass possible in a given time, then the volume of the sprouts would be important. On rights-of-way, however, the important considerations are probably the height of the sprouts and the number. DeBell and Alford (1972) carried out a comprehensive study on sprouting in eastern cottonwood (*Populus deltoides* Bartr.) from a five- to seven-year old plantation in the Mississippi River floodplain. After cutting on twelve occasions during the year (4- to 6-inch stumps were left) the sprouts that developed were counted and measured 24 months later. All growth data were adjusted to a 24-month base so that a valid comparison of sprout growth for different cutting dates could be made. The results obtained are given in Table V. For trees cut in May, June and July, the number of sprouts per stump, sprout height and sprout diameter were all very low, whereas for trees cut October through February the values were generally very high. The authors recommended that if sprouting is to be minimized, cutting should be conducted during the early growing season (preferably May or June).

TABLE V

EFFECT OF TIME OF YEAR OF CUTTING ON SPROUT PRODUCTION
IN EASTERN COTTONWOOD (*POPULUS DELTOIDES* BARTR.)

Month of Cutting	Sprouts per Stump	Sprout Height (ft) (tallest)	Sprout Diameter (bh)(in)
January	6.3	15.8	1.4
February	7.9	15.8	1.2
March	5.6	14.1	1.2
April	3.4	7.9	0.7
May	1.3	8.5	0.6
June	2.7	6.8	0.3
July	3.1	9.6	0.5
August	3.5	11.8	0.8
September	4.2	13.6	1.0
October	3.9	15.8	1.2
November	4.1	15.8	1.4
December	5.1	17.2	1.4

bh = breast height

Table taken from DeBell and Alford, 1972.

Belanger (1979) investigated the sprout production on five-year-old American sycamore (*Platanus occidentalis* L.) stumps after cutting on four occasions during the year (January, March, May and July). Every year for four years the number of live sprouts, and the height and diameter of the dominant sprout were recorded (see Table VI). The largest and heaviest sprout clumps resulted from cutting saplings in January and March. The least growth but largest number of sprouts per stump resulted from cutting in July. By the end of the fourth year after cutting, those saplings cut in July had slightly more live sprouts than saplings cut at any other time of the year, but the height of the dominant sprout was less than half that of the dominant sprout on stumps cut in January, March and May. Dry-weight production of fibre per acre after four years ranged from a high of 4074 kg from stumps cut in March to only 494 kg from stumps cut in July.

TABLE VI

SPROUTING RESPONSE OF AMERICAN SYCAMORE (*PLATANUS*
OCCIDENTALIS L.) STUMPS RELATED TO MONTH OF CUTTING

Month Cut	Variable	Mean Sprouting Response Per Stump, by Year After Cutting			
		1	2	3	4
January March May July	Live sprouts	Number			
		9.6	5.4	3.1	2.6
		9.0	5.1	2.8	2.4
		10.1	6.5	3.3	2.6
		14.9	8.7	6.1	4.0
January March May July	Diameter of dominant sprout	Inches			
		0.8	1.1	1.3	1.5
		0.9	1.1	1.4	1.6
		0.6	1.0	1.1	1.3
		0.2	0.5	0.6	0.7
January March May July	Height of dominant sprout	Feet			
		8.0	10.8	13.3	15.8
		7.9	10.9	13.9	16.7
		5.2	7.8	10.4	12.7
		1.8	3.7	5.0	6.1

Table taken from Belanger, 1979.

Although Roth and Hepting (1943) found no marked relation between the season of cutting and either the number of stumps sprouting or the number of sprouts per stump in three species of oak grown on plots in the George Washington National Forest in Virginia, there was a relationship between season of cutting and sprout height (see Table VII). With all those species of oak investigated sprout height (after four growing seasons) was smallest in trees cut in June and August.

For tree species which exhibit a seasonal variation in sprout production, sprouting (considered as survival, the number of sprouts or sprout weight) is usually maximal when trees are cut in winter and minimal when they are cut in mid-summer (Blake and Raitanen, 1981). In many instances it has been difficult to

compare different species because investigators have measured different parameters (eg, sprout height but not sprout volume). Blake and Raitanen (1981) have compiled a list of species in which summer cutting results in less vigorous sprouting than winter cutting (see Table VIII). There are several other species which do not show any seasonal variation in sprouting, and these include kola trees (*Cola nitida*) (Odegbaro, 1973), oak (*Quercus* spp) (Roth and Hepting, 1943) and sweetgum (*Liquidambar styraciflua* L.) (Wenger, 1953).

TABLE VII

RELATION OF SEASON OF CUTTING TO HEIGHT OF SPROUTS AT THE
END OF FOUR GROWING SEASONS IN SEVERAL OAK SPECIES

Species and Month Cut	Total Stumps (number)	Total Stumps Bearing Sprouts at End of Fourth Year (number)	Average Height of Dominant Sprouts at End of Four Growing Seasons (feet)
White Oak (<i>Quercus alba</i> L.)			
November	29	24	10.2
April	19	18	8.7
June	44	40	7.4
August	26	25	7.9
Black Oak (<i>Q. velutina</i> Lam.)			
November	29	27	13.4
April	27	22	12.7
June	27	22	8.4
August	37	26	10.3
Scarlet oak (<i>Q. coccinea</i> Muench.)			
November	28	28	11.9
April	19	17	11.4
June	18	13	8.7
August	26	20	9.1
All Species			
November	86	79	11.9
April	65	57	11.1
June	89	75	7.9
August	89	71	9.1

Table taken from Roth and Hepting, 1943.

TABLE VIII

SPECIES WHICH EXHIBIT MORE VIGOROUS SPROUTING
WHEN CUT IN WINTER RATHER THAN SUMMER

Species	Reference
Eastern cottonwood (<i>Populus deltoides</i> Marsh.)	DeBell and Alford, 1972
Quaking (or trembling) aspen (<i>P. tremuloides</i> Michx.)	Pringle et al, 1973
Flowering dogwood (<i>Cornus florida</i> L.)	Buell, 1940
American sycamore (<i>Platanus occidentalis</i> L.)	Steinbeck et al, 1972
<i>Eucalyptus obliqua</i>	Blake, 1972
Mountain ash (<i>E. regnans</i> F.Fuell.)	Cremer, 1973
Black Cherry (<i>Prunus serotina</i> Ehrh.)	Wendell, 1975
Northern red oak (<i>Quercus rubra</i> L.)	Wendell, 1975

Table adapted from Blake and Raitanen, 1981

4.0 FACTORS WHICH AFFECT ROOT SUCKERING4.1 Influence of Temperature on Formation
and Growth of Root Suckers

Trembling aspen (*Populus tremuloides* Michx.) generally reproduces vegetatively by suckers that arise adventitiously on lateral roots (Sandberg, 1951). Maini and Horton (1966) reported that maximum incidence and growth of suckers occurred on root cuttings of aspen that were maintained at 23°C. Above and below this temperature there was a gradual decline in the incidence and growth of suckers. Similar results were obtained by Sterrett et al (1968) with black locust (*Robinia pseudoacacia* L.) root cuttings. Temperatures above 25°C promoted the formation of more suckers than lower temperatures. Maini and Horton (1966) suggested that forest managers could readily perpetuate stands of high quality trembling aspen by taking measures which result in maximum soil temperatures, such as clear-cutting followed by ground scarification or burning. However, regeneration of poor stands could be prevented or reduced by maintaining tree or underbush cover and disturbing the ground as little as possible.

4.2 Influence of Season of Cutting on Root Suckering

Brinkman and Roe (1975) reported that when stems of trembling aspen (*Populus tremuloides* Michx.) were cut in the dormant season, more root suckers were obtained than if the cutting was performed in the growing season. Schier (1973) had earlier

reported a similar finding with the same species, although his results were not so impressive in that he found a wide variation in the number of suckers produced per cutting with different clones of aspen.

In an earlier study on the effect of season of cutting on resprouting and suckering of trembling aspen (*Populus tremuloides* Michx.) Stoeckeler (1947) found that when 10-year-old trees growing on a poor site were cut in June, fewer sprouts and suckers came up than if the trees were cut in December, April or August (see Table IX). Stoeckeler (1947) did not distinguish between stem sprouts and root suckers, however it is probable that the majority of the stems that he counted were root suckers. He also found that the average height of the sprouts and suckers was lower in trees cut in June and August than in trees cut in December and April (Table IX). This reduction in the number of sprouts and suckers produced after June cutting was not so apparent in a similar experiment carried out with 16-year-old trees growing on a good site, where he found only a 30% decrease in the number of sprouts and suckers present five to six years after cutting in June.

TABLE IX

EFFECT OF TIME OF YEAR OF CUTTING ON SUCKER AND SPROUT PRODUCTION OF TREMBLING ASPEN (*POPULUS TREMULOIDES* MICHX.)*

Season of Cutting	Aspen Stems per Acre		Increase or Decrease (%)	Average Height, Aug 1945 (ft)
	Dec 1939 (number ¹)	Dec 1945 (number ²)		
December 1939	5193	6153	+18	4.7
April 1940	3407	3573	+5	4.0
June 1940	6680	1560	-77	2.8
August 1940	4070	4207	+3	3.0

¹ Tally several days before cutting

² Values represent total number of aspen suckers or stump sprouts five to six years after cutting.

* Trees were grown in the Nicolet National Forest in north eastern Wisconsin.

Table taken from Stoeckeler, 1947.

Sterrett et al (1968) have reported that in black locust (*Robinia pseudoacacia* L.), the number of suckers produced on cuttings taken in June was considerably lower than the number on cuttings taken in January, March, August or November. These authors suggested that this lack of vigor in June may be attributed to the low availability of carbohydrate reserves.

4.3 Effect of Double Decapitation on Root Suckering

Stoeckeler (1947) reported that a double cutting of stems of trembling aspen (*Populus tremuloides* Michx.) in June, first at 100 cm above the ground and then at 30 cm after an interval of 3 or 24 h, may be more effective at reducing both the number and the size of subsequent root sucker and stump sprout growths than a single decapitation (see Table X). As described previously, Stoeckeler (1947) did not distinguish between sprouts and suckers, but the majority of the stems he counted will have been root suckers. Stoeckeler (1947) also obtained similar results when the cutting was carried out in August, when a double cutting resulted in a 2% decrease in suckering and sprouting while in a single cutting there was a 36% increase in the number of suckers and sprouts.

4.4 Influence of Carbohydrate Reserves on Root Suckering

Schier and Zasada (1973) found that there was no correlation between the number of suckers produced on root cuttings of Alaskan and Utah aspen (*Populus tremuloides* Michx.), taken at various times of the year, and the concentration of total nonstructural carbohydrates in the roots. Similar results had been obtained earlier by Tew (1970). Thus although carbohydrate reserves are undoubtedly necessary for aspen shoot outgrowth, there appears to be no correlation between sucker numbers and carbohydrate content of roots. This is similar to the situation with stump sprouting, where again carbohydrate reserves do not appear to control numbers or growth of sprouts (discussed in an earlier section).

5.0 PHYSIOLOGICAL EFFECTS OF CUTTING WOODY SPECIES

5.1 Decapitation Leads to "Rejuvenated" Trees

As a woody plant grows older and larger, branching becomes more complex and plant vigor declines (Borchert, 1965; 1976). However treatments such as decapitation, severe pruning and defoliation cause a return of various characteristics to the "juvenile" stage, notably a great increase in seedling vigor (Smith, 1965; Blake, 1980).

TABLE X
EFFECT OF CUTTING TREMBLING ASPEN
(*POPULUS TREMULOIDES* MICHX.) SPROUTS AND SUCKERS
IN JUNE BY FOUR METHODS

Method of Cutting	Aspen Stems per Acre		Increase or Decrease (%)	Average Height, Aug 1945 (ft)
	Dec 1939 (number ¹)	Dec 1945 (number ²)		
Cut twice at 3-h intervals	2256	702	-69	2.4
Cut twice at 24-h intervals	1578	1220	-23	2.2
Cut once, high stump 100 cm	1810	1574	-13	4.0
Cut once, low stump 30 cm	2384	2136	-10	5.0

¹ Tally before any cutting was done

² Values represent total number of aspen suckers or sprouts
5½ years after clearcutting

Table taken from Stoeckeler, 1947.

As a juvenile plant grows up, structural differences along its stem axis may reflect the gradual change from juvenile to mature types of growth. The presence of juvenile types of morphology at the base of an apple seedling and graded levels of increasing maturity up the tree were pointed out by Passecker (1949). Evidence of the presence of transitional stages between juvenility and maturity in beech trees has been developed by de Muckadell (1959). In Passecker's original concept the juvenile form of a fruit tree extended up from the base to a point approximately halfway up the stem and extended some way outwards along the lowermost limbs. Mature tissues existed at the tips of the mainly uppermost branches, while intermediate tissues connected these to the juvenile tissues lower down the plant. The morphological graduation from juvenile to mature forms of fruit trees is associated with a gradual increase in the ability of the tree to form flowers. Such a graduation is also evident in the leaf and stem forms and in the ability to transmit the physiological expression of juvenility to cuttings or graft sections taken

from various parts of the plant (Leopold and Kriedemann, 1975). De Muckadell (1959) attributed the maturity gradient from the base to the top of a mature tree to the progressive aging of a meristem as it grows. Thus meristems left at the base of the tree retain the stage of juvenility which existed in the meristem at the time the laterals were established. The meristem which has grown entirely through to the top of the tree has aged in proportion to the extent of its growth. The most mature meristems are therefore at the apex of the tree and at the ends of its longest branches (Leopold and Kriedemann, 1975).

Juvenile oak (*Quercus* spp) and beech (*Fagus* spp) trees tend to have a delayed abscission of leaves until spring. In older trees the juvenile characteristic of leaf retention may be very evident in lower branches, even though the upper branches are mature (de Muckadell, 1954).

The coppice method of regeneration (where hardwoods are cut down and the stump sprouts prolifically) has been used for forest production for many centuries because of the exceptional early growth rates of the stump sprouts compared with seedlings of the same age (Daniel et al, 1979; Blake, 1980). The decapitation of trees under the coppice method of regeneration effectively removes the most mature parts of the tree and leaves the most juvenile parts, and for this reason the trees are said to be "rejuvenated". Such decapitation severely disturbs physiological functions which rely on photosynthesizing area, water, and plant growth regulator balances. After decapitation some species sprout prolifically. Others like *Eucalyptus obliqua* L'Her., although sprouting initially, eventually die within three to six weeks after decapitation (Blake, 1981a). There is no convincing physiological explanation of the rejuvenation which occurs following coppice treatment or the observation that some species survive decapitation whilst others do not (Blake, 1981a). It has been hypothesized (Daniel et al, 1979) that the phenomenal early growth of some decapitated trees is due to the advantage conferred by the established root system and the production of some unspecified wound hormone. The initial advantage that a sprout has over a seedling, which builds its own root system, is lost since the sprout is confined to part of the parental root system and this loses efficiency with age (Daniel et al, 1979).

5.2 Root and Shoot Relationship in the Intact Plant

Before considering what happens to root/shoot relations after decapitation and the transport of plant growth regulators from the root to the shoot and vice versa after decapitation, the relationship between the shoot and the root in the unadulterated plant must be described.

The internal control of growth involves close interdependency between roots and shoots as sources of growth requirements (Kramer and Kozlowski, 1979). Roots depend on leaves for photosynthetic products and plant growth regulators such as auxins and gibberellins. Shoots depend on roots for supplying water, minerals, and certain plant growth regulators such as cytokinins (Skene, 1975) and gibberellins (Kramer and Kozlowski, 1979).

It is a commonplace observation that a growing apical bud inhibits the development of other lateral shoot buds, but whether this influence is transmitted via the supply of inorganic and organic nutrients and/or in the form of one or more plant growth regulators is uncertain. It has proved extremely difficult to distinguish between possible correlative roles of various factors (eg, nutrients and plant growth regulators) as they affect lateral bud outgrowth and their undoubted involvement in biochemical events within the buds themselves (Phillips, 1975). The most obvious treatments which allow previously inhibited buds to grow out are those which involve either complete removal of the growing apical bud or prevention of its growth by physical means (Phillips, 1969). Such knowledge does not in itself allow any conclusion to be drawn as to whether the correlative signal is nutritional and/or a plant growth regulator since an active apical bud is both a source of the plant growth regulators auxin and gibberellin and also a sink for nutrients (Sheldrake, 1973). Stem-girdling treatments have shown that interruption of the continuum of living cells along the stem (by either ringing or heat-girdling) usually results in outgrowth of lateral buds situated below the girdle, and yet at the same time the upper portion of the shoot continues to grow and consume nutrients and water (Harvey, 1920; Snow, 1925). This suggests that lack of growth by lateral buds is attributable to the downward movement through living tissues of an influence originating in the apical part of the shoot, and not to their starvation of nutrients or water.

It seems likely that the correlative signal in apical dominance has a plant growth regulator basis. Nutrients and water are not unimportant in that growing buds obviously require these substances, and it is known that nutrient and water levels can affect plant growth regulator levels and distribution in the plant (Phillips, 1975). It has been reported that inorganic nutrient supply to roots influenced auxin synthesis in the apical bud and cytokinin, gibberellin and abscisic acid levels have been found to be markedly affected by water potential in the plant (for a review see Phillips, 1975). Cytokinin, gibberellin and abscisic acid (all examples of plant growth regulators) are synthesized primarily in the roots, meristematic tissue in the shoot and root, and the leaves, respectively.

Treatment of lateral buds on a decapitated plant with cytokinins or gibberellins (Phillips, 1975) commonly results in an increased rate of lateral bud growth. Both of these plant growth regulators are antagonistic to auxin, in that auxin inhibits the growth of lateral buds. Ethylene, another plant growth regulator, promotes aging and senescence (Abeles, 1973). There is much evidence to suggest that some or all of the plant growth regulators mentioned above may act in concert during processes such as release from bud dormancy and leaf senescence and abscission.

5.3 Root and Shoot Relationship Following Decapitation

When woody plants are cut off at the base, what happens to the delicate balance in the source sink relationship of the shoot and root?

Although much work has been done on the consequences of decapitation in herbaceous species, little work has been reported using woody species. Decapitation may be regarded as a drastic removal of the apical meristem, and hence many investigators have concentrated on the subsequent interruption in the downward movement of auxin produced by the apical meristem. Eliasson (1969, 1971 a,b,c) looked at the amount of auxin in the roots of aspen (*Populus tremula* L.) following removal of the growing shoot parts. He found that sucker formation on the roots occurred when auxin levels were low. When Eliasson (1971b) examined the auxin content of roots of whole aspen plants he found that it varied throughout the year, with the highest auxin level being found during the period of shoot growth (May, June and July), and that during this period the capacity of root segments to form suckers was low. Earlier experiments with aspen (*Populus tremula* L.) (Eliasson, 1961) trembling aspen (*P. tremuloides* Michx.) bigtooth aspen *P. grandidentata* Michx.) (Farmer, 1962) and black locust (*Robinia pseudoacacia* L.) (Sterrett and Chappell, 1967) had shown that treatment with IAA (3-indolylacetic acid - a natural auxin) reduced or prevented sucker formation from the roots. In both aspen and black locust it was reported that the presence of stump sprouts reduced or prevented root suckering (Eliasson, 1971c, Sterrett and Chappell, 1967). In the latter study the seedlings were cut either 2.5 cm above the root collar to leave a stump (on which sprouts developed) or 2.5 cm below the root collar to leave a "root stub" (on which no sprouts developed, but suckers developed on the roots). These authors concluded that auxin synthesized in the leaves of the intact plant or in the buds of the stump sprouts inhibits root suckering in the same manner as the terminal bud (apical meristem) inhibits lateral bud growth on stems. When IAA was applied to the cut surface of black locust root stubs, root suckering was prevented for as long as IAA was

replenished. The same concentration of IAA applied to the cut surface of the stump did not significantly retard stump sprouting. This agrees with Thimann's findings (Thimann, 1937 - discussed in detail in Ontario Hydro Research Division Report No 82-153-K) that roots are more sensitive to auxin than are stems or buds.

In a recent study Taylor et al (1982) examined the decapitation of *Eucalyptus camaldulensis* Dehn and *E. obliqua* L'Herit seedlings, which may either promote vigorous growth (in the former) or cause rapid senescence and death (in the latter). Seedlings of both seedlings were either decapitated or decapitated with a small upwardly directed shoot left on the stump. Previous work (Blake, 1981a) had shown that if one small, upwardly directed lateral shoot was left on the cut stump (or a certain concentration of IAA was applied) susceptible *E. obliqua* seedlings could survive decapitation. Decapitation did not markedly alter the relatively high amounts of gibberellins in roots and shoots of *E. obliqua*, the susceptible species, although increased levels of gibberellins were observed in the stumps of seedlings left with one shoot after decapitation (Taylor et al, 1982). The overall levels of gibberellins were relatively low in the roots and shoots of the resistant *E. camaldulensis* but higher in the shoots. Cytokinin-like activity was initially low in all tissues, but increased dramatically in stump and root tissue following decapitation. Increases ranged from approximately 5-fold (stump tissue of either species, minus-shoot treatment) to approximately 40-fold (shoot tissue of the resistant *E. camaldulensis* seedlings left with one shoot). In both species ethylene production increased to a peak seven days after decapitation provided a shoot had been retained. This ethylene peak preceded a marked upturning of the retained shoot, and was not present in the stumps of totally decapitated seedlings. For totally decapitated seedlings ethylene evolution in *E. obliqua* (susceptible species), but not *E. camaldulensis* (resistant), had ceased by 15 days. Ethylene can promote aging and senescence in many plants (Abeles, 1973). Although both intact and decapitated *E. obliqua* plants senesce quickly and die in the presence of ethrel, an ethylene-releasing compound (Blake, unpublished data), ethylene evolution in the totally decapitated *E. obliqua* seedlings (which did not survive) decreased during final senescence following a brief burst of ethylene production two days after decapitation.

Since decapitation of both *E. obliqua* and *E. camaldulensis* led to a large increase in cytokinin-like activity in the stem and/or shoot, it is probable that such an elevation is a necessary component of growth renewal (Taylor et al, 1982). In a number of woody species endogenous cytokinin activity has been shown to increase significantly prior to bud-burst, for example, in xylem

sap of *Populus X robusta* and willow (*Salix viminalis* L.) (Hewett and Wareing, 1973; Alvim et al, 1976) bud tissue of sugar maple (*Acer saccharum* Marsh.) and *Populus X robusta* (Taylor and Dumbroff, 1975; Hewett and Wareing, 1973) and stem tissue of sugar maple (Dumbroff and Brown, 1976). Increased levels of cytokinins have also been induced by defoliation of *Theobroma cacao* L. (Alvim et al, 1974) and girdling of weeping willow (*Salix babylonica* L.) (Van Staden and Brown, 1978), processes which lead to eventual growth of formerly quiescent buds.

From the study (Taylor et al, 1982) on endogenous hormone levels and earlier work involving the application of exogenous hormones (Blake, 1981b) the following overall pattern of hormone involvement in the recovery of decapitated eucalyptus seedlings has been suggested (Taylor et al, 1982). Cytokinin-like activity increased markedly within one week of decapitation and cytokinins promote the growth of quiescent buds. Subsequent development and elongation of newly formed shoots would then depend in part on increased gibberellin synthesis (or release) and metabolism. If a lateral shoot was allowed to remain at the time of decapitation, this shoot began to turn upwards (hyponastic response) following an observed peak of ethylene production and assumed the position of a new leader. The increase in ethylene production could possibly be induced by high cytokinin levels (Abeles, 1973). This sequence of plant growth regulator activity occurred in both species of *Eucalyptus*. *E. camaldulensis* appeared to have a somewhat greater capacity for cytokinin production and gibberellin metabolism than did *E. obliqua*, although differences between the two species were only observed if a shoot was left following decapitation. These differences may reflect the intrinsic ability of the two species to produce or metabolize these plant growth regulators (thus to re-establish growth rapidly), which in turn may reflect the differential survival rate.

Although not investigated by Taylor et al (1982), other workers have examined the role of abscisic acid in the breakage of bud dormancy. Unlike other plant growth regulators, abscisic acid is basically a growth inhibitor. It accumulates in at least some kinds of woody plant under short photoperiods, and application of abscisic acid to some perennials causes dormancy. Taylor and Dumbroff (1975) reported that although abscisic acid occurs in both roots and stems of sugar maple (*Acer saccharum* Marsh.), changes in concentration were not correlated with the breaking of dormancy. Alvim et al (1978) also reported that abscisic acid levels in willow (*Salix viminalis* L.) were not significantly changed by photoperiod and these authors suggested that this hormone may not play a role in bud dormancy. In a recent review, Powell (1982) concluded that even though there is little evidence to support the possible role of abscisic acid

in regulating shoot growth, it would be unwise to conclude that it has no important role to play. It may well be exerting a strong influence through systems not reflected in the kind of research commonly reported.

5.4 Growth of Sprouts Following Decapitation

After decapitation of most hardwood trees, the sprouts which develop on the cut stump grow a great deal more quickly than the stems on the intact plant (Blake, 1980). Blake (1980) examined such sprout growth in *Eucalyptus camaldulensis* seedlings after decapitation. Stump sprouts from decapitated seedlings showed a threefold increase in the rate of stem elongation, a doubling in transpiration rate per seedling, and a five- to eight-fold increase in transpiration per unit leaf area compared with intact seedlings. Reversion to a more juvenile leaf morphology following decapitation was accompanied by a decrease in leaf stomatal resistance. The increased transpiration rate following decapitation (compared with intact seedlings) was apparently explained by increased stomatal length and higher stomatal frequency on the lower surface of sprout leaves. The rapid growth of sprouts on stumps of hardwood species found in North America has not been examined in such detail.

6.0 CONCLUSIONS

1. Many species of woody plant produce sprouts on the lower stem and root collar in response to the sudden death of the parent top as a result of cutting, fire, disease or physiological disorders. These stump sprouts usually arise from previously existing dormant buds.
2. Removal of the parent top by decapitation causes the remaining stump to be "rejuvenated", and the sprouts that develop on the stump grow a great deal more quickly than the stems on the intact plant.
3. A smaller number of woody species regenerate by root suckers following disturbances such as heavy cutting or fire. These root suckers originate from adventitious buds on roots of the residual and cut plant.
4. Many factors influence the number and rate of growth of sprouts and suckers that develop on the stumps and roots of woody species after removal of the parent top. Among those that affect sprouting in some tree species are tree age, diameter and height of the cut stump, the time interval between successive cuttings, and the time of year of cutting. Root suckering is affected by soil temperature and

the season of cutting. Decapitation of many tree species in the winter leads to vigorous sprout and sucker development.

5. Although changes in the levels of plant growth regulators in the stem and roots following decapitation have not been thoroughly investigated, it appears that cytokinin and gibberellin are necessary for the development and elongation of sprouts and suckers. Auxin inhibits the development of sprouts and suckers. The involvement of ethylene and abscisic acid in the development of sprouts and suckers has not been determined.
6. In both clearcutting and routine maintenance of some Ontario Hydro rights-of-way it may prove to be more effective to cut certain woody species in the summer, since the number and rate of growth of sprouts and suckers that develop is lower than if cutting were carried out in the winter.

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APPENDIX A

DORMANT AND ADVENTITIOUS BUDS

The difference between dormant and adventitious buds has been described by Kozlowski (1971). Only some of the buds present on a tree in winter (called winter buds) produce shoots whereas the rest remain dormant, sometimes throughout the life of the tree. Dormant buds often persist in large numbers. Old dormant buds may eventually develop into shoots, or they may finally die. Often they enable a tree to survive as they are stimulated to grow by fire, injury or removal of actively growing buds above them. If young tender leaves of new shoots are killed by early spring frosts, new ones often develop from dormant buds. However, whether dormant buds become active depends on the degree of defoliation. In trembling aspen (*Populus tremuloides* Michx.), for example, refoliation occurred only in trees in which defoliation was essentially complete (Rose, 1958).

Most investigators agree that dormant buds, originally located in leaf axils of twigs, are thereafter connected to the pith by a bud trace. They remain undeveloped under the bark and grow only enough each year for the tip to keep pace with cambial growth. Hence a dormant bud really consists of an encased, modified branch which may later be stimulated to sprout.

Buds which form rather irregularly on older portions of a plant and not at the stem tip or in the leaf axil are called adventitious buds. These form on parts of the root or stem which have no connection to apical meristems. They vary as to origin and may spring from deep-seated tissues or peripheral ones. For example, adventitious buds may arise from callus tissue around wounds, in the cambium, or from mature tissues in the endodermis or pericycle region (MacDaniels, 1953). The important distinction between adventitious and dormant buds is the lack of a bud trace all the way to the pith in the former.

Many adventitious buds arise from mature tissues near or adjacent to a wound. They usually produce a shoot without going through a dormant period, with their activity apparently regulated by hormone balance (Eliasson, 1961). The cambium of stumps of poplar (*Populus*), beech (*Fagus*), and walnut (*Juglans*), often proliferates to produce callus in which bud primordia originate and develop into adventitious shoots. Adventitious buds also occur commonly on roots of many species including black locust (*Robinia pseudoacacia*), ailanthus (*Ailanthus altissima*) and sumac (*Rhus*) (Romberger, 1963), but not on their boles or branches. Vasilevskaya and Kondratjeva (1955) studied

adventitious buds in 34 species of woody plants which are reported to sucker. Adventitious buds were found on all but eight of these species, and they were always located in areas where dieback of lateral roots occurred.

POOR

QUALITY

ORIGINAL

